CROTON BIGBENDENSIS TURNER (EUPHORBIACEAE) REVISITED

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ABSTRACT

B.L. Turner separated from the widespread *Croton dioicus*, a new species characterized by more luxuriant stem growth with long internodes and narrower leaves occurring on well drained soils in the Big Bend region of trans-Pecos Texas. Turner's new taxon differs only in a few quantitative (not qualitative) characters, and in these characters it blends into *C. dioicus*. Turner's taxon is considered to be minor variant in a wide-ranging and variable species. Turner's original species description does not meet the requirements for being validly published because two holotypes were designated.

RESUMEN

B.L. Turner distinguió una nueva especie, caracterizada por su crecimiento más exuberante, con entrenudos largos y hojas más angostas, creciendo en suelos bien drenados, en la región del Big Bend de trans-Pecos, Texas, separándola de *Croton dioicus*, especie de amplia distribución. El taxón nuevo propuesto por Turner difiere solamente en unos pocos caracteres cuantitativos (no cualitativos) y, en estos caracteres, se intergrada con los de *C. dioicus*. Se considera al taxón de Turner como una variante secundaria de una especie variable de amplia distribución. La descripción original de la especie nueva de Turner no cumple con los requisitos de publicación válida puesto que se designaron dos holotipos.

INTRODUCTION

Croton dioicus Cav. [*C. neomexicanus* Müll.Arg.] (Euphorbiaceae) is a wide ranging, distinctive, dioecious perennial of *Croton* section *Drepadenium* (Raf.) Müll.Arg. (Webster 1993). The species is characterized by twice dichotomous styles, valvate, eglandular sepals, petals absent, moderately short petioles, and leaves with a distinctive silvery canescence formed by fringed peltate scales 0.3–0.5 mm in diameter. The species occurs from west-central and trans-Pecos Texas and adjacent New Mexico, southward into arid regions of Mexico in the states of Chihuahua, Coahuila, Nuevo León, Tamaulipas, Veracruz, Durango, Zacatecas, San Luis Potosi, Hidalgo, Tlaxcala, México, Puebla, and Oaxaca.

Turner (2004) distinguished from *C. dioicus*, a separate species, with the epithet "bigbendensis," characterized as being a larger, bushier plant, with longer upper-stem internodes and linear-lanceolate leaves 5–7 times as long as wide. He noted that the species is restricted to areas along the Rio Grande in Hudspeth, Presidio and Brewster counties of Texas (with one specimen cited from adjacent Coahuila, Mexico) becoming dominant in sandy habitats. He further noted that the species does not occur with *C. dioicus*, and where they are "near contact" they do not appear to intergrade. He considered his new species to be a good "cryptic" or "biological" species. All the characteristics used to delineate the proposed species were quantitative; no qualitative characteristics were noted or implied.

Unfortunately, in his paper he cites two herbarium specimens as holotypes, one pistillate (*Turner 22-204A*) and one staminate (*Turner 22-204B*), each given a separate number. Though collected at the same time from the same population (a single gathering), the International Code of Botanical Nomenclature (McNeill et al. 2006) does not allow two separate specimens with two separate numbers to be designated as separate holotypes [ICBN Art. 9.1–"A holotype of a name or a species or infraspecific taxon is the **one** specimen or illustration used by the author, or designated by the author as the nomenclatural type (emphasis mine)] and thus the name was not validly published and is considered an invalid name (Kanchi Gandhi, pers. comm.; see International Plant Name Index). A holotype can consist of more than one sheet of a single specimen (ICBN Art. 8.3) if clearly noted, and can consist of more than one plant in a single gathering (Art 8.2), but

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the designation of two separately numbered specimens, mounted on separate sheets, each named as holotype (Turner 2004, pp. 81 & 82), renders the specimens syntypes (Art. 9.4, ex. 1) and therefore no holotype exists and the name is not validly published.

As his proposed new taxon occurs within the Chihuahuan Desert, my area of interest, I analyzed characteristics used by Turner (2004) to distinguish the two taxa using specimens he annotated in the TEX-LL herbarium. I initially measured total stem length and maximum internode length as an indication of plant size, leaf blade length and width as well as petiole length from one larger leaf on each specimen. I also recorded soil type (clay, gypsum, or sandy-well drained) for each collection when noted on the label. Petiole length and total stem length, while quite variable, were not further used because the petiole length generally correlated with leaf size and the total stem length displayed in specimens too often reflects the portion collected, not total plant size. Data on soil type were very spotty from specimens outside west Texas so this was not used in the analyses but is discussed below. While criticism can be raised from taking measurements from herbarium specimens, these are the specimens used to make taxonomic decisions and, while imperfect, they represent samples of a species and they are readily available.

METHODS

Data were collected from all specimens at TEX-LL (*n*=296) with 41 from trans-Pecos Texas identified by Turner as "Croton bigbendensis" plus six of my specimens that are clearly referable to that taxon, 72 from typical *Croton dioicus* in trans-Pecos Texas (west of the River), 98 from *C. dioicus* from cis-Pecos Texas (east of the Pecos River) and adjacent New Mexico, and 85 from *C. dioicus* from Mexico. For the quantitative analysis measurements of longest internode (in mm) present on each specimen, as well as the longest leaf length and its width (in mm) and these were used to formulate a leaf length/width ratio.

RESULTS

Measurements of maximum internode length in mm (abscissa) graphed against a ratio of leaf length/leaf width indicating leaf shape (ordinate) are shown in Figure 1. Collections of putative "*Croton bigbendensis*" are distinguished by open circles; those of *Croton dioicus* are indicated by solid shapes with those from trans-Pecos Texas indicated by solid circles, from cis-Pecos Texas by solid squares, and those from Mexico by solid triangles.

The means and standard deviations of four characteristics recorded from the "bigbendensis" specimens, from the specimens from each of the three areas of *C. dioicus* and from all combined *C. dioicus* are presented in Table 1. While the means of leaf and internode lengths are distinctive, the large standard deviations indicate the wide variation found in *Croton* "bigbendensis."

The graph (Fig. 1) shows that while many specimens of "*bigbendensis*" are characterized by long internodes and/or narrow leaves, the measurements blend into those of *C. dioicus*—there are not two distinct clusters of data points indicating well defined character differentation, and a fourth (10 of 41) of the "bigbendensis" data points are nested within those of *C. dioicus*. The specimens of the proposed taxon "bigbendensis" have leaf l/w ratios averaging 5.9, ranging from 3–14.4, and maximum internode lengths averaging 50.0 mm ranging from 31–98 mm. Specimens assignable to *C. dioicus*, in contrast, have leaf l/w ratios averaging 3.5, ranging from 1.4–6.8, and maximum internode lengths averaging 30.4 mm, ranging from 11–72 mm. Both features exhibit strong quantitative overlap.

Throughout the geographical range of *Croton dioicus* there is much variation in plant habit, leaf shape and leaf and internode size (Fig. 1). In growth form plants range from low, woody-based subshrubs with erect new growth, to plants that die back to the base and produce erect-ascending shoots that eventually fall and give rise to upright lateral shoots during the growth season. In most plants the basal leaves are largest and the terminal, younger leaves are progressively smaller and often narrower. Leaf shape ranges through broadly ovate, elliptical, oblong-ovate, oblong-elliptic, oblong-lanceolate, linear-lanceolate, and linear. Plants from central Texas and northeastern Mexico have broader, more ovate, moderate- to large-sized leaves

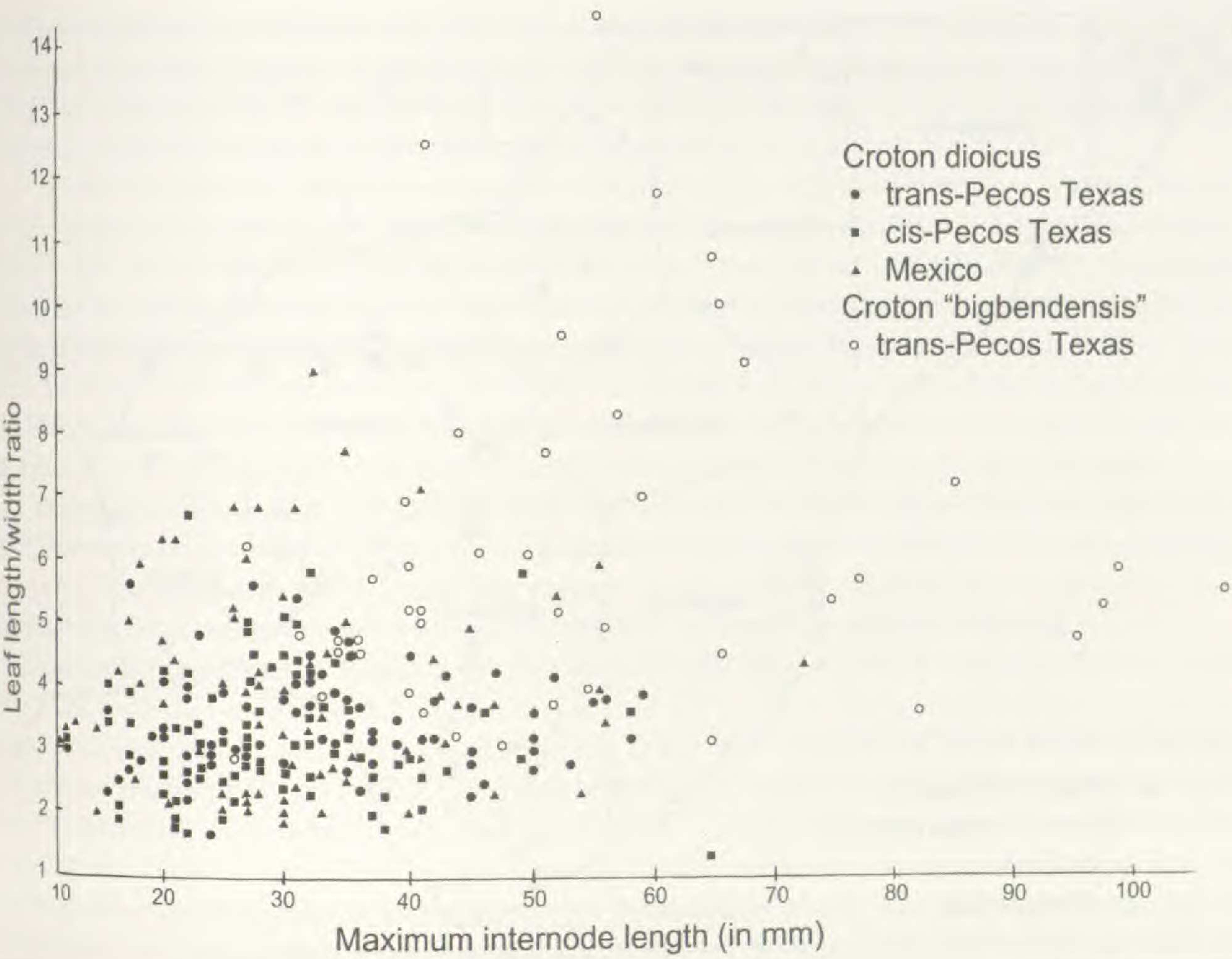

Fig. 1. Graph showing relation of leaf blade length/width ratio vs. maximum internode length (in mm). Measurments taken from 294 specimens at TEX-LL herbarium. Not all overlapping data points are shown.

Table 1. Means and standard deviations of measurements taken of the longest leaf (length, width, and lenght/width ratio) and the longest internode of each specimen annotated as "bigbendensis" by Turner, and each specimen of *Croton dioicus* from trans-Pecos Texas, cis-Pecos Texas, and Mexico. All *C. dioicus* specimens are combined.for the mean and standard deviation of "dioicus-all collections".

Taxon	count	Lf length-mm	Lf width-mm	Lf. L/W ratio	Internode length
"bigbendensis"	41	35.3 ± 10.0	6.3 ± 2.0	5.9 ± 2.4	50.0 ± 19.5
dioicus-trans-Pecos	72	25.4 ± 6.7	7.7 ± 2.1	3.4 ± 0.8	32.0 ± 11.2
dioicus-cis-Pecos	98	23.4 ± 5.2	7.7 ± 2.2	3.2 ± 0.9	29.3 ± 10.2
dioicus-Mexico	85	24.9 ± 7.3	7.1 ± 2.4	3.8 ± 1.5	30.4 ± 11.4
dioicus-all collections	255	24.5 ± 6.4	7.5 ± 2.2	3.5 ± 1.2	30.4 ± 10.9

Those of desert habitats often have more numerous, smaller leaves, but in years of good rainfall they may develop large leaves and strong terminal growth. Overall, the leaves of *C. dioicus* in trans-Pecos Texas are oblong-elliptical to elliptical ovate but are otherwise very similar to those of "bigbendensis."

Figure 2 shows the distribution of plants of *Croton dioicus* and "bigbendensis" in trans-Pecos Texas based on specimens annotated by Turner (2004). *Croton dioicus* is indicated by solid circles and well differentiated "bigbendensis" (i.e. those with narrower leaves and/or long internodes) are shown as open circles, and the location of those specimens annotated as "bigbendensis" by Turner, but nested with *C. dioicus* in Figure 1, are designated by open squares. This map differs from that of Turner (2004) as it shows the two taxa growing

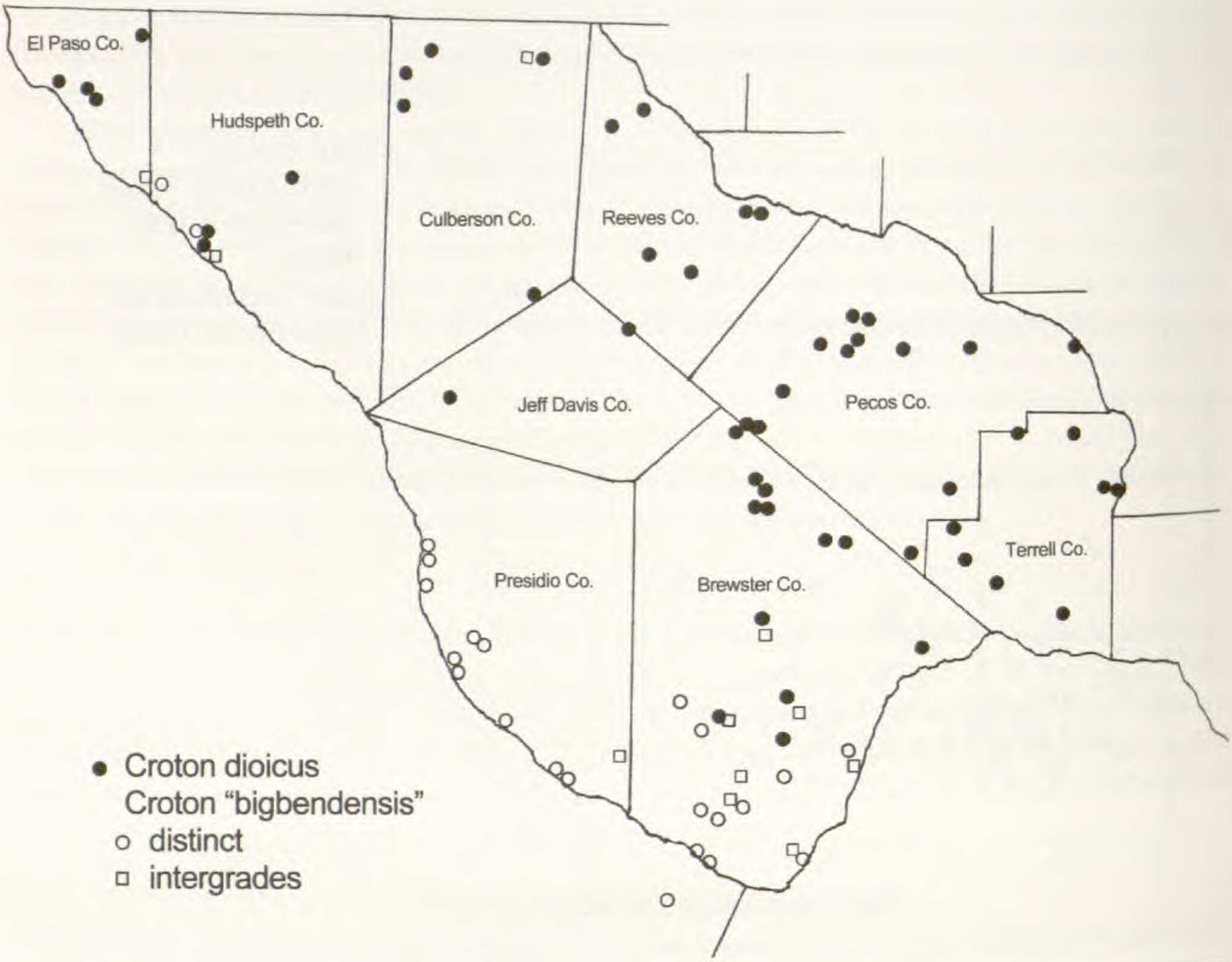

Fig. 2. Distribution of *Croton dioicus* and "bigbendensis" in trans-Pecos Texas, based on specimens so identified by Turner at TEX-LL.

in close proximity in southeast Hudspeth and central Brewster counties. There are collections within the range of "bigbendensis", annotated by Turner as *C. dioicus* that were not shown in his map: (1) Brewster Co., Chisos Mts. to Coopers Store (= Persimmon Gap), *Lundell & Lundell 13294* (LL), with internodes to 40 mm long, leaves to 32 × 10.5 mm (l/w ratio 3.0); (2) Persimmon Gap, *Warnock 5/2/37* (TEX), with internodes to 35 mm, leaves 27 × 5.7 mm (l/w ratio 4.7); (3) 21 mi s of Marathon, *Ertter 4707* (TEX), with internodes to 46 mm; leaves 27 × 6 mm (l/w ratio 4.5) and Nine Point Mesa, Webster and Westlund 32586 (TEX) with internodes to 52 and leaves 26 × 9.2 mm (l/w ratio 2.8). These have shorter internodes and/or broader leaves than typical "bigbendensis" and are shown in figure 2 as *C. dioicus*.

There are also collections of *C. dioicus* well outside of the range of Turner's "bigbendensis" that are also similar to his proposed new species: (1) Culberson Co. Guadalupe Mt. area, *Correll & Johnston 24260* (LL), with internodes to 56 mm, leaves 36 × 9.5 mm (l/w ratio 3.8) to 20 × 3.4 mm (l/w ratio 5.8); 41 mi N Van Horn, in gypsum, *Correll & Johnston 18360* (LL) with internodes to 31 mm, leaves 33 × 6 mm (l/w ratio 5.5); (2) southeast Hudspeth Co., Finlay to McNary, in sand, *B.H. Warnock 13668* (TEX), with internodes to 55 mm, leaves 51 × 13 mm (l/w ratio 3.8). These are basically robust plants of sandy-gravelly habitats with large but broader leaves.

In Mexico, a collection from the Samalayuca dunes south of Cd. Juaréz, Chihuahua (*M. F. Roberts s.n.*, TEX) with internodes to 80 mm; leaves 27 × 7 mm (l/w ratio 3.8) seems to compare well with "bigbendensis" except that the leaves are overall shorter. Specimens from the state of Hidalgo all had linear to narrowly oblong leaves with l/w ratios from 3.9–7.9, and longest internodes from 18 to 52 mm. Likewise specimens from Puebla also had narrow leaves with l/w ratios of 3.9–6.3, but internodes 27–55 mm in maximum length. Some specimens from Nuevo León, also compare well with the proposed "bigbendensis," e.g., *Urbatsch 1019* (TEX), with internodes to 41 mm, leaves 37 × 5.2, (l/w ratio 7.1), showing that the characteristics used by Turner to establish his new taxon were by no means restricted to the Big Bend area of Texas.

The one characteristic that was not possible to analyze is that of growth habit. Most *Croton dioicus* in Texas is suffrutescent-suffruticose, woody at the base, with herbaceous stems above forming bushes to about 2–3 dm tall, with the size reflecting water resources of the season. Plants of "bigbendensis" are typically larger. Turner (2004) notes the hight of "bigbendensis" as 4–5 dm. However, *Lott et al. 5588* [Presidio Co., Texas (TEX)] notes growth habit as a single-stemmed shrub to 1 m tall, *Turner 24-351* [Hudspeth Co. Texas (TEX)] includes a photograph of a bushy plant ca. 1 m tall and wide. I have seen plants in the foothills of the Chianti Mts. (Presidio Co., Texas) with long lax stems that are initially erect but that eventually fall over and produce erect sucker shoots to form low rounded plants about 3 dm tall but 12 dm in diameter.

Regarding substrate, most of the specimens of "bigbendensis" are from sandy or otherwise well drained soils, but others are from clay-limestone flats and hillsides and still others are from roadsides etc. Label data is missing on some specimens or is otherwise vague as to the soil type. There are several collections from Brewster Co.,Texas that were noted coming from clay flats, or limestone substrates-hillsides.

Two collections made by Turner in 2004 in gypsum soils in northeastern Culberson County, Texas (Fig 2) illustrate the problem with Turner's interpretation of the taxon. *Turner 24-409* (TEX) is a pistillate plant considered to be *C. dioicus* that has oblong-ovate leaves with rounded tips, 26.5 × 8.2 mm (l/w ratio 3.2) and internodes to 42 mm long. It is growing with/near a staminate specimen (*Turner 24-402*) (TEX) that has lanceolate, acute-tipped leaves, 31 x 6.5 mm (l/w ratio 4.7) with internodes to 46 mm long that is identified as "bigbendensis." The two specimens appear identical in stature, coloration etc. and both are in flower. But while the specimen he considers to be "bigbendensis" is well out of its normal range (Fig. 2), the specimen of *C. dioicus* bears a hand-written note by Turner "growing with *C. bigbendensis* (24-402); no intermediates seen." I see this as just variation within a population of *C. dioicus*.

Turner's *Species Concepts*: Turner (in Turner 2001; Turner et al. 2003; Turner 2004) advocates the biological species concept implying that his species have some degree of biological (i.e., reproductive) isolation sensu Mayr 1969, 1992. At the same time, in his personal discussions, he speaks of the importance eco-geo-morphological factors (or morpho-eco-geographic integerity, Turner 2001) in species recognition in which species may differ ecologically i.e., occur in different habitats, or in different soil types (gypsum, sand) or be geographically isolated (disjunct) and/or have some morphological discontinuity or a combination of these features. His primary rank for infraspecific taxa is variety, with subspecies reserved only for clustering groups of varieties if the need arises sensu Holmgren (1994) and Turner and Nesom (2000). He notes that varieties are subunits of a species that are geographically separate and generally morphologically distinguishable, but in Turner's concept they **must** show intergradation with related taxa to be varieties: if he sees no intergradation, they are considered distinct species (Henrickson 2004).

The concept that varieties must show intergradation is where Turner departs from others. He considers his interpretation as modern in contrast to Old-School definitions where varieties are used for minor varients of a species as defined in Correll and Johnston (1970) and Diggs et al. (1999). But I think it is safe to say that most botanists today recognize varieties (or subspecies) as subunits of a species that have a geographical component (Stuessy 2009) but without such regard to the presence or absence of intergradation. And then there is the separate question of whether all variation found in wide-ranging species needs to be recognized nomenclaturally. But Turner's varietal concept does explain why he publishes so many new species.

It is expected that all outbreeding species will exhibit some degree of variation, and that in peripheral populations, selection would favor those individuals best adapted to any new biotic or abiotic environmental parameters. Over time, all populations tend to move toward adaptation to their current environment. In small populations, these changes can be enhanced, sometimes in a non-adaptive way, by genetic drift (Grant 1963). If the location of an outlying population differs in substrate or in moisture availability, you would expect changes reflecting adaptation to this new environment. But even if adaptive characteristics become fixed in an outlying population, does this make the population a distinct species?

In this particular instance, *Croton dioicus* of northern trans-Pecos and adjacent portions of central Texas mostly occurs in clay flats in which much of the rainfall runs off quickly, and the plants tend to be short, low rounded specimens adapted to a seasonally severe environment. In areas of sandy-gravelly substrates, the water can penetrate deeply, providing a reservoir of water for later development. Rhyolitic substrates can form coarse gravels-sands that also accumulate rainwaters. Other sandy habitats in this region occur along the Rio Grande. An increase in moisture availability would favor those plants that could grow larger and produced more flowers and fruits over a season. This would not require any novel gene-based changes, but rather would simply favor those plants within a population that produce more growth-regulating substances (auxins etc.) that would in turn promote more robust plants with longer internodes and stems and leaves, characteristics that would not be adaptive in drier sites. Since the southern portion of the southwestern trans-Pecos Texas has volcanic (not limestone) mountains, and has other sandy habitats along the Rio Grande, the sandy-gravelly habitats tend to be geographically separated.

With Turner's eco-geo-morphological concept, he finds ecological, geographic and morphological differences between the clay- vs. sandy-substrate populations. But he notes that his new species is a biological species sensu Mayr (1969, 1992), though providing no evidence that the two taxa have any reproductive isolation. His map (Turner 2004) shows the two taxa as completely allopatric, but using his own specimens as mapped here in figure 2 (some added after his publication), they are not completely allopatric except in the sands along the Rio Grande in Presidio Co., Texas.

What we are dealing with in "bigbendensis," appears to be a derivative series of populations in well drained soils that differ only in quantitative characteristics from those on primarily clay substrates. In characteristics of vestiture, flower, and fruit, and time of anthesis, they are identical to the widespread *C. dioicus*. Quantitative characters can be used to establish species if there are no or reduced overlapping values (Luckow 1995). But as shown in Fig. 1, the values of C. "bigbendensis" merge strongly with those of *C. dioicus* making recognition at the species rank, in my opinion, untenable. As noted above, measurements of 10 of the 41 specimens recognized by Turner as "bigbendensis" are nested well within the specimens of *C. dioicus* (Fig. 2) and others are closely peripheral. Even if these were to be considered *C. dioicus* and "bigbendensis" were redefined as only those plants with longer internodes and/or narrower leaves, "bigbendensis" would still consist of an amalgamation of plants, some with narrower leaves and others with longer internodes, that would not separate from the variation in *C. dioicus*.

There is another problem associated with such quantitatively defined "taxa." In times of good rains, the plants can show strong growth with long leaves and internodes. But under poor growth conditions, the plants may be stunted with shorter internodes and smaller leaves and some of the plants nested within *C. dioicus* in figure 2 may be just that. Also, the first-formed leaves of a growth season are typically broader than those formed later in the season.

But while the data do show the existence of plants with narrower leaves and longer internodes in the southern margin of trans-Pecos Texas, the plants are not clearly distinguished from *C. dioicus*. Due to the blending of the quantitative characteristics used to define "bigbendensis," using Turner's own criteria (Turner and Nesom 2000), the taxon would be considered a variety of *C. dioicus*. But, I see no reason to recognize "bigbendensis" at any rank, but to incorporate it's characters into the known variation of the wide ranging and poorly studied *Croton dioicus*. As it stands, *Croton dioicus* is a very distinctive species, easily recognized over its range by substantial characters. I see no value in recognize peripherial populations that differ in minor quantitative characters as equal species. Certainly in this instance there is no evidence that "bigbendensis" is a good biological species. But we must remember that even with field observations, without experimental data, such taxonomic decisions are just opinion.

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